

**RESILIENCE OF ALPINE MAMMALS TO WEATHER ANOMALIES ASSOCIATED
WITH CLIMATE CHANGE**

FINAL REPORT

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ABSTRACT – Although increased frequency of extreme-weather events is one of the most-secure predictions associated with contemporary climate change, effects of such events on distribution and abundance of climate-sensitive species remain poorly understood. Montane ecosystems may be especially sensitive to weather anomalies because of complex abiotic and biotic interactions that propagate from climate-driven reductions in snowpack. Snowpack not only provides insulation from extreme cold, but also influences forage availability through timing of melt-off and water availability. We related relative abundances of two species of alpine mammals, the American pika (*Ochotona princeps*) and hoary marmot (*Marmota caligata*), to measures of weather and snowpack dynamics over an 11-year period that included a year of record-low snowpack in Washington, USA. We sought to 1) quantify any change in mammal abundance associated with the snowpack anomaly, and 2) identify aspects of weather and snowpack that influenced inter-annual abundance of pikas and marmots. Whereas relative abundance of pikas declined markedly at elevations below 1400 m, it increased slightly at higher elevations that retained snow during the low-snow winter. Pikas showed a 1-year lag response to the snowpack anomaly suggestive of reproductive failure at low elevations following the weather anomaly, rather than direct mortality from exposure to extreme cold, in the absence of snowpack. Relative abundances of marmots declined by 69% between 2007 and 2016; the most-severe losses occurred at warm, dry sites. Moisture was surprisingly important, evidenced by strong support for top-ranked models that had interactions of vapor pressure deficit with snowpack duration (pikas) or cold exposure (marmots). Notably, our novel application of vapor pressure deficit from gridded climate data for analyses of animal abundances shows strong potential for improving species distribution models. A *post-hoc* assessment of vegetative phenology and productivity indicated that mammals were affected more strongly by physiological stress rather

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than biotic interactions associated with weather and snowpack dynamics; however, responses were context-dependent and species specific. Our results indicate that weather extremes, warming temperatures, and increasing aridity can lead to rapid loss of species in montane ecosystems.

INTRODUCTION

Climate change poses one of the greatest challenges to conservation of biodiversity because temperature and precipitation are fundamental to ecological niches, and recent warming has propagated complex abiotic and biotic interactions that can alter species assemblages [1,2,3]. Biotic responses to climate change have been documented worldwide and include changes to species' geographic distributions [4,5], elevational distributions [6,7,8], phenology [9,10], phenotype [11,12], genotype [13,14,15], and behavior [16]. Rates of change in many ecosystem components have been nonlinear, and many have increased markedly since the 1970s [17,18]. Many species responses to climate change, such as latitudinal shifts in distribution, have followed expectations based on life-histories, but more-nuanced patterns of change, such as movement to lower elevations, have also been documented [7,19,20]. Mechanistic understanding of biotic responses to climate change is needed to disentangle responses to climate from other factors like habitat loss. Despite extensive evidence of change to biotas from recent climate change, few studies have identified the mechanistic relationships driving those changes [21]. Although many studies have related changes in species to long-term averages of temperature and precipitation, such metrics are likely proxies for the underlying mechanism of exposure to chronic- or extreme-weather events associated with climate change that affect populations and their distributions.

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Increasing occurrence and severity of extreme weather events are among the most-certain of predicted outcomes associated with contemporary climate change [22]; however, little is known about how biotic responses to weather extremes vary across species, ecological context, and gradients of weather severity. Weather extremes can reveal species vulnerability to climate change through exposure to environmental conditions that test physiological limits or through modification of essential resources. Effects of weather can be direct through exposure to temperature extremes and water stress, or indirect through biotic interactions, such as altered forage production and phenological mismatches [23,24]. Producers and primary consumers often respond directly to weather, whereas higher-level consumers are more likely to be influenced by biotic interactions [25]. Mechanistic responses of species to weather extremes like drought or flooding are well-known [26,27], but species' responses to many extreme conditions associated with climate change remain uncertain. The ability of species to adapt to change decreases with increasing and less-predictable environmental change [28], which underscores how fundamentally challenging climate-based extreme events could be for conservation of biodiversity.

Snowpack reductions associated with climate change [22,29] are exacerbated by extremely warm weather and could transform montane ecosystems by affecting water availability, vegetation, animal movement, phenology, and protective cover for subnivean biota [30,31]. Snowpack has already decreased significantly over the past century, and years of extremely low snowpack due to unusually warm temperatures, as seen recently in western North America, are expected to become more common [22,29,32,33]. Such snowpack anomalies could reveal the sensitivity of species to extreme weather and provide insight on biotic responses to climate change.

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Montane ecosystems have many properties that can reveal the variability in species responses to weather and climate change, as these ecosystems are often remote and insulated from most anthropogenic land uses and effects. Topographic complexity, inherent to montane ecosystems, creates sharp ecological gradients that include short growing seasons and harsh weather. Diverse species inhabit montane ecosystems and vary in their adaptations to winter conditions and snowpack. Some strategies to cope with winter conditions (e.g., hibernation) may be more resilient to weather extremes than others (e.g., hoarding, seasonal migration), and mechanisms that govern species populations may vary across coping strategies. Understanding the variability in resilience to weather extremes and mechanistic relationships across species can inform conservation strategies like managing for climate refugia [34].

Ecological consequences of changing snowpack dynamics are evident across trophic levels [35,36,37] throughout Arctic and alpine ecosystems [31,38]. Many alpine mammals that depend on snowpack are important to ecosystem function as herbivores and prey for several wildlife species [39,40,41]. American pikas (*Ochotona princeps*) and hoary marmots (*Marmota caligata*) can be useful indicators of change in alpine ecosystems because they are climate-sensitive and differ in their life-history strategies for winter survival [18,42,43,44]. Marmots hibernate, whereas pikas are active throughout winter and hoard food to survive. Pikas have been extirpated from about 44% of sites that were occupied prior to 1991 in the hydrographic Great Basin, where heat exposure has best explained range retractions [18,43,45]. However, pika abundances have varied with snowpack in other regions [46,47,48]. Less is known about hoary marmots, but snowpack influences reproductive success [49,50], and abundances of other marmot species vary with snowpack dynamics [49,51,52,53,54]. Hypothesized mechanisms for such relationships include fatal exposure to extreme cold in the absence of snowpack [55]. Alternatively or in

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addition, altered phenology of principal forage species for pikas and marmots may extend periods without green vegetation and lead to starvation [56].

We related relative abundances of American pikas and hoary marmots to weather and snowpack dynamics over an 11-year period that included a year with record-low snowpack [32,33] in winter 2014-2015 (hereafter, winter 2015) to 1) quantify effects of low snowpack and 2) evaluate hypothesized mechanisms that could influence population dynamics of these species. We developed novel predictors for models that represented the interactive effects of temperature, precipitation, moisture, and snowpack on mammal abundances. We hypothesized that abundances of pikas and marmots following the winter weather anomaly would be lower than previous years, and that differences would be best explained by inter-annual variation in snowpack (Figure 1). We also expected that winter weather dynamics would explain more variation in mammal abundances than summer conditions because of the abundant snowfall and mild summer temperatures typical for our study area in Washington, USA. Our results revealed nuanced responses to winter weather and snowpack dynamics that advance understanding of species responses to weather anomalies and climate change. Notably, our analyses of moisture and animal abundances, to our knowledge, are unprecedented and suggest strong potential of new gridded climate surfaces for vapor pressure deficit (VPD) to explain animal distributions.

METHODS

2.1 Study area

The North Cascades National Park Service Complex (hereafter, the Park), which comprises North Cascades National Park, Ross Lake National Recreation Area, and Lake Chelan National Recreation Area, is located in north-central Washington, USA and consists of roadless

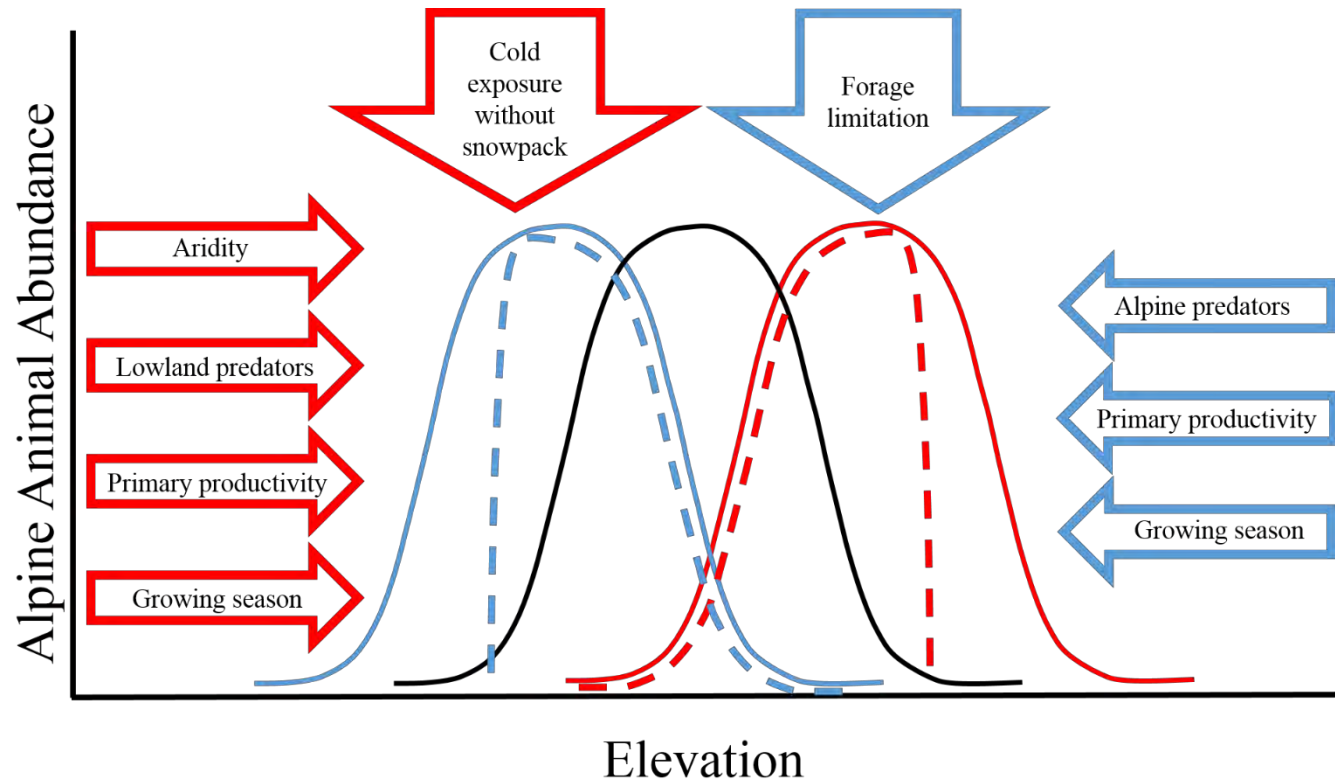


Figure 1. Suitable habitat areas for a mountain-dwelling species can shift across years. Hypothesized effects of below- (red line) and above-average (blue line) snowpack on abundance of alpine animals are shown relative to the abundance pattern in a normal snow-year (black line) in an idealized montane ecosystem. The influence of factors that limit animal abundance at lower- (red arrows) and upper-elevational (blue arrows) bounds may shift along the elevation gradient, depending on snowpack. At high elevations, limits to forage availability and animal distributions from persistent snowpack, for example, can extend to lower elevations in years of above-average snowpack. Primary productivity at high elevations can increase in years with little snow, unless frost damage limits growth. Cold exposure without snowpack may occur across a wide elevation band in cold years with little snow, but within a narrow band in warm years. Where shifts to high or low elevations (dashed lines) are biophysically limited by habitat (e.g., soil suitability, forage availability, mountaintop), animal abundances may shift to a truncated distribution.

wilderness except for one road bisecting the Park. Steep mountains with conifer forests dominate the Park, where elevations range from 100 m to 2800 m. Annual precipitation ranges from 50 to 500 cm based on proximity to mountain divides [57], and several vegetative life zones reflect wet, dry, or subalpine conditions [58]. Weather station data from 2003-2017 at Thunder Basin (elevation 1317 m; 48.52 latitude, -120.98 longitude; [59]) indicated that mean maximum temperatures ranged from 17.6°C to 23.6°C in summer. Mean minimum ambient temperatures ranged from -7.3°C to -3.4°C in winter. Days of snow cover ranged from 174 days to 239 days, and the date of snow melt occurred between 13 May and 27 June. The weather anomaly in winter 2015 created the shortest duration of snowpack and earliest date of melt-off during this period. The second shortest duration of snowpack was 196 days, which melted off 21 May 2004.

2.2 Field methods

In 2016, we resurveyed sites of pika and marmot occurrence from previous studies in the Park to measure relative abundance of these mammals for our assessment of weather and snowpack dynamics, including the record-low snow year in 2015. In 2009, Bruggeman [48] surveyed pikas at 30, 1-km² sites that were distributed within 3 km of roads or trails, following a stratified random design based on location relative to mountain-range divides and classes of low (<914 m), moderately low (914-1218 m), middle (1219-1523 m), moderately high (1524-1827 m), and high (\geq 1828 m) elevation. Each site comprised \geq 1 talus patches. In 2016, we surveyed a stratified subset of 13 sites with 58 talus patches that had annual measures of relative abundances of pikas during 2009-2013 inclusive. We also surveyed pikas at another set of 11 sites, each of which comprised 1 talus patch that was surveyed from 2013-2015 (A. Beers, *unpublished data*). These 11 sites were distributed along 3 elevational transects that ranged from 465-1700 m, and were part of a study on pika genetics [60].

For marmots, Christophersen [61] randomly selected 31 sites along trails >1220 m in elevation and within vegetation classes deemed suitable for marmots. Most of these sites were surveyed in 2007, and the remaining sites were surveyed in 2008, which yielded 19 sites with marmot detections [61]. In 2016, we resurveyed marmots at 79 point-count stations distributed across the same 19 sites. We repeated marmot surveys at these same sites in 2017 to supplement our data from 2016.

To ensure estimates of relative abundance were comparable across years, we adopted methods specified in previous studies ([48,61], A. Beers, *unpublished data*). To count pikas, surveyors walked parallel transects spaced 10 m apart and covering each talus patch within each site. All 122 surveys from 2009 to 2016 occurred between July 7 and October 24, with 8%, 60%, 30%, and 2% of surveys performed in July, August, September, and October, respectively. Similar survey methods have yielded detection probabilities >0.90 for pikas [18,62], and we concentrated survey efforts during mid to late summer to minimize any seasonal biases in detectability. Although snow could limit access to some sites until mid-summer, correlation of survey date with elevation was low ($r = 0.21$). Estimates of relative abundance were based on the number of detections by sighting, vocalization, and active haypile presence (i.e., green vegetation present). For the 11 sites along elevation transects, we also included fresh scat as an indicator of current pika occupancy, following the protocol from previous years. Multiple haypiles <25 m apart were attributed to a single pika because their territories are exclusive and typically cover <2,000 m² [48,63]. We paid close attention to avoid double counting by noting and geo-referencing pika detections during surveys. Locations of old haypiles were documented but did not contribute to estimates of relative abundance.

For marmots, we conducted point counts at stations within the 19 sites where marmots were previously detected by Christophersen [61]. Stations occurred at approximately 400-m intervals within meadow habitats deemed suitable for marmots. To minimize any seasonal biases in detection probabilities, all surveys from 2007 to 2016 occurred in July or August, with the exceptions of one survey on 26 June 2007 and one on 5 September 2007. Surveys in 2017 occurred from August 8 to September 13, with 42 percent of surveys in August. Correlation of survey date with elevation was low ($r = -0.23$). Detection probabilities for hoary marmots have varied among studies, ranging 0.22 to 0.96 [50,64,65]. Surveyors used binoculars to search meadows and boulder fields from each station for 30 minutes between 07:00 and 12:00 to record all marmot detections based on visuals and vocalizations. When marmots were detected, we classified individuals as adults, juveniles, or subadults (1-2 years old) based on size, color, and behavior [51,66,67,68]. Adults were much larger in size than subadults or juveniles and had darker coloration on the face and back with a deep-brownish-colored tail. Subadults were medium-sized with lighter pelage, whereas juveniles were small with light-colored pelage and had unique behaviors including attempts to nurse.

2.3 Weather and snowpack data

We characterized weather and snowpack dynamics at each site with metrics of temperature, VPD, precipitation, and snow water equivalents (SWE) from gridded climate surfaces for 2003-2016 (see predictor definitions in Table A.1). For most predictors, we used daily metrics of temperature extremes, VPD extremes, and precipitation from PRISM (Parameter-elevation Relationships on Independent Slopes Model) at 800-m spatial resolution [69]. We obtained daily measures of SWE at 1-km resolution from Daymet [70] to characterize snowpack. Our predictors for summer weather expressed growing-season precipitation, VPD, and exposure to chronic (i.e.,

mean daily maximum temperatures for July-August) or acute (i.e., number of days >25 °C) heat. Minimum values of VPD typically coincided with the minimum temperature and inversely represented chronic dryness. Sites that achieved zero deficit experienced condensation, which can have important implications for biota through water availability. We used maximum values of VPD to represent the severity of dryness at a site, which might index acute stress from dehydration. Minimum and maximum VPD in summer had low correlation ($r = 0.03$), indicating that these metrics represented distinct aspects of moisture.

For winter weather, our predictors expressed snowpack duration, VPD, and exposure to acute (i.e., number of days with temperature <-10 °C) or chronic (i.e., mean minimum temperature from November-February) cold either throughout the year, or expressly at times without snowpack (acute = minimum daily temperature; chronic = number of days with temperature <0 °C; Table A.1). We defined snowpack presence as SWE ≥ 30 mm because snow depths >20 cm provide insulation for pikas [71] and our threshold corresponds to snow depth of approximately 10 cm for snowpack of moderate density (300 kg m^{-3}), typical in the North Cascades [72]. We expected that VPD minimums and maximums would represent exposure to chronic and acute dryness in winter, respectively. In addition, cold exposure would be accentuated at sites with low minimum VPD in winter [73]. Correlation between minimum and maximum VPD during winter was also low ($r = 0.36$). All predictors were standardized to a normal distribution with a mean of 0 and standard deviation of 1 for the analysis.

2.4 Analytical methods

We related relative abundance of pikas and marmots to measures of weather and snowpack dynamics with *a priori* regression models that represented specific, hypothesized mechanisms of influence on distributions of these species (Table A.2). We used generalized linear models with

mixed effects in R package *lme4* to analyze counts of pikas and marmots from each year of the study. We used a Poisson distribution for analyses of marmot counts and a negative binomial distribution for pika counts to account for over-dispersion. Each model had the study site as a random effect to facilitate the analyses of repeated measures. We related counts of pikas and marmots from each year to the summer conditions during the survey or to the winter conditions that immediately preceded the pika surveys for that year. In addition, we evaluated models with predictors that represented a 1-year lag effect by relating counts to weather and snowpack conditions of the previous year. Analyses assumed constant detectability for pikas and marmots over the study period.

We tested whether the relative abundance of pikas and marmots changed after winter 2015 with the interaction between elevation and the time of survey, defined as before or after winter 2015. Like many temperature-based predictors, snowpack duration was correlated with elevation, so we tested both types of interactions to determine whether measures of the snowpack anomaly explained more variation in relative abundance of pikas and marmots than elevation. For these tests and others on the significance of predictors in mixed-effects models, we used Type II Wald chi-square tests in the R *car* package.

Models in the *a priori* sets for pikas and marmots represented either summer or winter conditions with ≤ 3 predictors (Table A.2). We excluded combinations of highly-correlated predictors ($r \geq 0.75$) within models. All univariate models were candidates. No multivariate models included more than one predictor of heat or cold exposure because of correlations among temperature-based predictors. Exceptions were the combination of cold exposure predictors with those that expressed cold exposure without snowpack. Several models tested interactions between VPD and exposure to temperature extremes or snowpack duration. We also tested

interactions between growing-season precipitation and heat exposure. To explicitly test whether responses of different species to the low-snow anomaly were mediated by different factors across species, model sets between species were identical. Model selection and inference followed an information-theoretic approach, where support for hypotheses was based on Akaike information criteria for small sample sizes (AIC_c) and Akaike weights [74]. We also assessed model fit with marginal and conditional coefficients of determination (R^2) from the R *piecewiseSEM* package for Poisson models [75] and following an R script for negative binomial models from Nakagawa et al. [76]. The marginal R^2 measures the variation explained by only the fixed effects, whereas the conditional R^2 measures variation explained by fixed and random effects combined.

We tested whether winter weather and snowpack conditions in 2015 differed from other years in our data set from 2003 through 2016 with linear mixed-effects models and Type II Wald F tests with Kenward-Roger estimates for degrees of freedom [77]. Each model included site as a random factor to account for the repeated measures and an indicator variable that identified observations from 2015. We used chi-square tests to compare ratios of juvenile to subadult to adult marmots counted during surveys in 2007 or 2008, 2016, and 2017. Gridded climate surfaces for 2017 were not available to include marmot counts from 2017 in our formal assessment of weather and snowpack effects. Therefore, we performed a separate analysis that included the marmot counts in 2017 to determine whether results of our analyses of marmot counts from 2007 to 2016 were robust. This analysis was limited to 1-year lag models from the *a priori* model set and alternative models that had 2-year lags for the 2017 marmot counts to assess further the effect of winter 2015.

RESULTS

3.1 Pikas

We detected 3,156 pikas from 2009 through 2016. Changes in relative abundance of pikas after the low-snow year of 2015 depended on elevation ($\chi^2_1 = 10.9$, $p < 0.001$): relative abundances generally decreased at low-elevation sites, but increased at sites above 1400 m (Figure 2A, C). Elevation was correlated with many of our climate predictors including snowpack duration in 2015 ($r = 0.87$), and elevation alone explained nearly as much variation in relative abundance of pikas as did the snowpack duration of 2015 (Figure 2B, D; $\chi^2_1 = 13.6$, $p < 0.001$, $\Delta\text{AIC}_c = 1.27$). Patterns in relative abundance of pikas suggested that the shift in relative abundance occurred after the summer of 2015, rather than immediately after the winter of 2015. The top-ranked model for pikas included the positive interaction between snowpack duration and winter VPD minimum with a 1-year lag effect (Table 1), indicating that relative abundance of pikas increased with winter-time dryness and snowpack duration (Figure 3). The model explained 85% of the conditional variation (i.e. fixed and random effects) and 10% of the marginal variation (i.e., fixed effects) in relative abundance of pikas. The top-ranked model had strong support (Akaike weight = 0.65), and the second-best model was not equally plausible ($\Delta\text{AIC}_c = 2.4$). Relative abundance of pikas was influenced more strongly by winter, rather than summer, weather dynamics (Table 2); models for pikas with predictors of winter weather or snowpack dynamics had a cumulative Akaike weight of 0.90. The best model based on any aspect of summer weather was not competitive ($\Delta\text{AIC}_c \geq 6.3$) and had an Akaike weight < 0.03 .

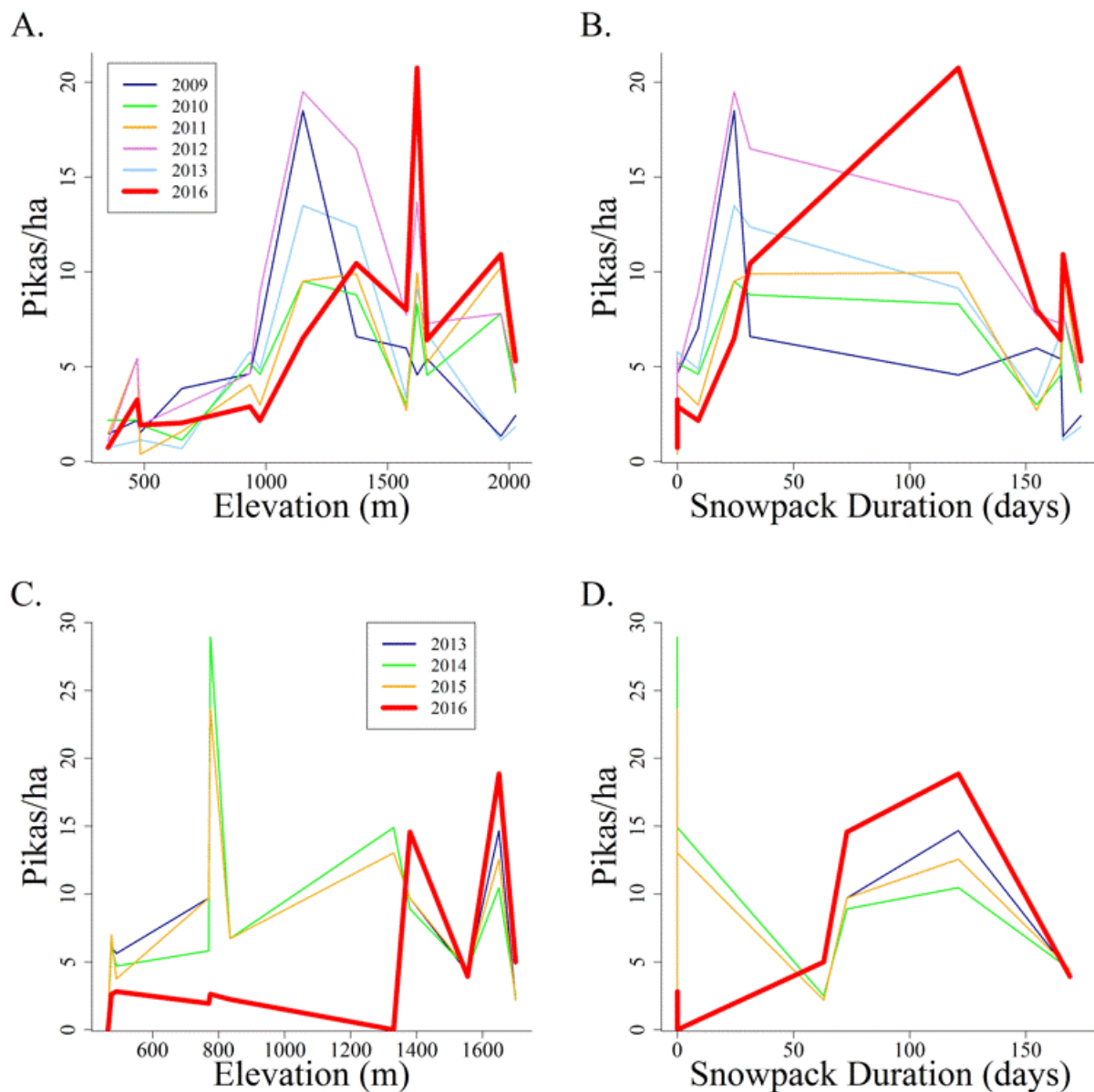


Figure 2. Relative densities of American pikas with elevation and snowpack duration in winter 2015 at 13 sites surveyed 2009-2013 and 2016 (A, B), and a different 11 sites surveyed 2013-2016 (C, D) at North Cascades National Park, Washington, USA. We calculated relative density for each site in each year as the number of pikas counted divided by area of talus within sites.

Table 1. Differences in Akaike's information criterion for small sample sizes (ΔAIC_c), model weights (w_i), and variation explained (R^2_c = conditional, R^2_m = marginal) for the 3 top-ranked models plus the null model in analyses for relative abundance of American pikas and hoary marmots at North Cascades National Park, Washington, USA, 2007-2016.

Model ^a	Species	ΔAIC_c	w_i	R^2_c	R^2_m
Winter VPDmin * Snowpack Duration	Pika	0	0.651	0.85	0.10
Winter VPDmin * Chronic Cold	Pika	2.42	0.194	0.85	0.09
Summer VPDmin + Acute Heat + GSP	Pika	6.30	0.028	0.81	0.19
Null	Pika	14.1	0.001	0.83	0
Winter VPDmax * Chronic Cold	Marmot	0	0.655	0.88	0.77
Winter VPDmin * Snowpack Duration	Marmot	2.27	0.322	0.88	0.83
Winter VPDmin * Chronic Cold	Marmot	4.25	0.119	0.87	0.70
Null	Marmot	119	<0.001	0.57	0

^aMinimum vapor pressure deficit = VPDmin. Maximum vapor pressure deficit = VPDmax. Growing-season precipitation = GSP. All models in this table had predictors that represented 1-year lag effects. Models with interactions included main effects for each interacting predictor.

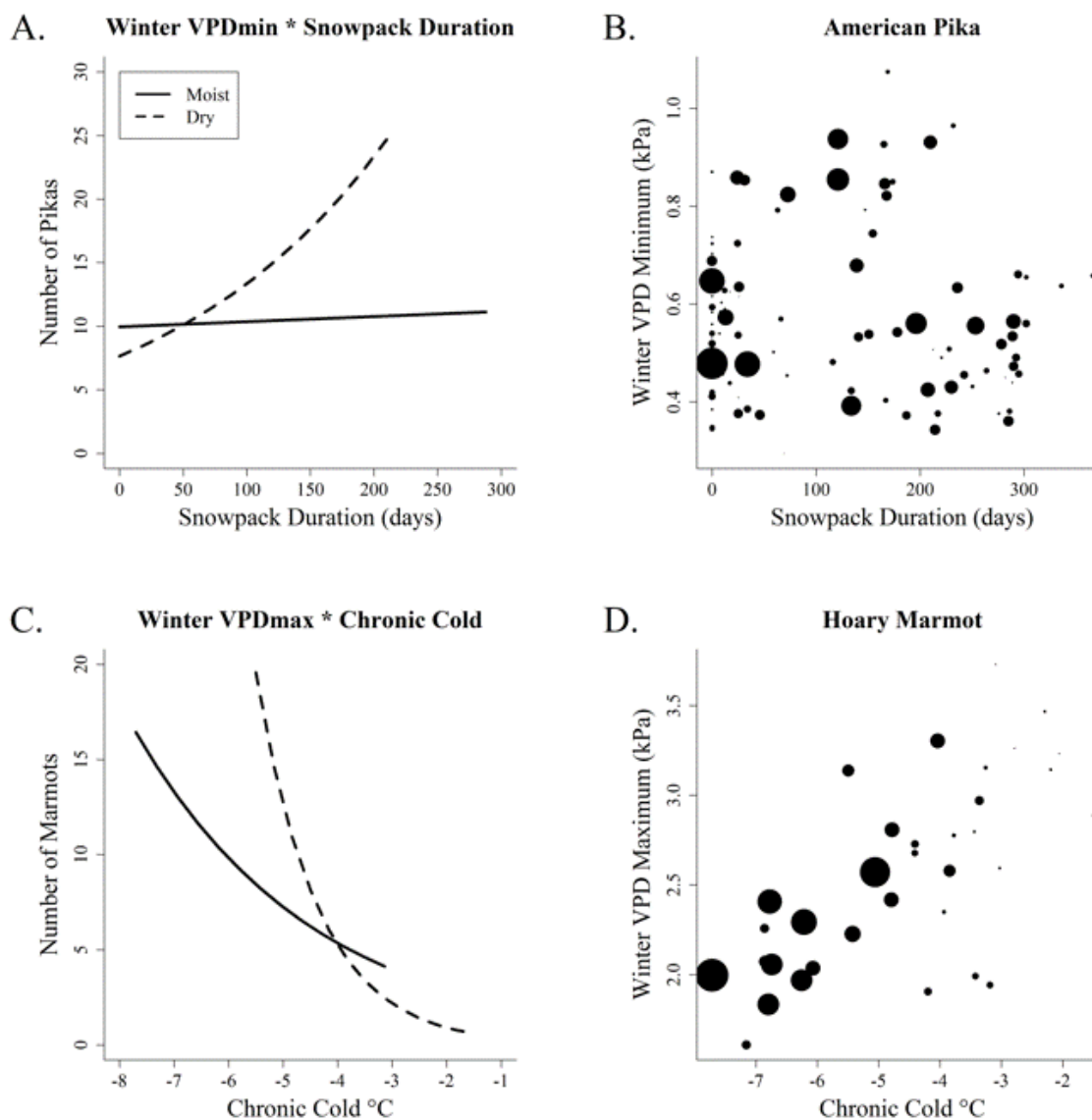


Figure 3. Predicted values from the A) best model for relative abundance of American pikas, as explained by the interaction of winter VPD minimum and snowpack duration; B) the relative density of pikas with winter VPD minimum and snowpack duration; C) the best model for relative abundance of hoary marmots, as explained by the interaction of winter VPD maximum and chronic cold; and D) the relative abundance of marmots with winter VPD minimum and chronic cold in the analyses of relative abundances for pikas and marmots at North Cascades National Park, Washington, USA, 2007-2016. Mean intercepts for the random sites were used for each prediction of pika or marmot abundance. Moist and dry prediction lines are based on the upper and lower 90th percentile values of winter VPD minimum observed within each dataset. Predictions cover the approximate range of values for the combination of VPD and snowpack or chronic cold observed in the datasets. Point sizes in B and D increase with increasing relative abundance of pikas or marmots. We calculated the relative density of pikas as the number of pikas counted at each site in each year divided the by the area of talus at each site.

Table 2. Coefficient signs of predictors and sums (w^+) and means (\bar{w}_i) of Akaike weights of models with each predictor in analyses of relative abundances of American pikas and hoary marmots in North Cascades National Park, WA, USA, 2007-2016.

Predictor	Season	Pika			Marmot		
		w^+ ^a	\bar{w}_i	Sign ^b	w^+	\bar{w}_i	Sign
Acute heat (days)	Summer	0.040	0.008	-	0 ^c	0	-
Chronic heat (°C)	Summer	0.023	0.005	-	0	0	-
Growing-season precipitation (mm)	Summer	0.056	0.007	+	0	0	-
Min vapor pressure deficit (kPa)	Summer	0.056	0.011	+	0	0	2+,1-
Max vapor pressure deficit (kPa)	Summer	0	0	-	0	0	+
Acute cold (days)	Winter	0.005	0	-	0	0	+
Chronic cold (°C)	Winter	0.212	0.030	-	0.735	0.105	-
Acute cold without snowpack (°C)	Winter	0.003	0	+	0	0	4+,1-
Chronic cold without snowpack (days)	Winter	0.002	0	-	0	0	-
Snowpack duration (days)	Winter	0.666	0.111	+	0.223	0.037	+
Min vapor pressure deficit (kPa)	Winter	0.865	0.079	+	0.292	0.027	2+,4-
Max vapor pressure deficit (kPa)	Winter	0.014	0.001	+	0.661	0.060	2+,4-

^aSigns and Akaike weights are from models with 1-year lags because models without the time lag did not have weights >0.001.

^bCoefficient signs were consistent across all models, unless the number of models with positive and negative signs is listed (e.g., 2+,1-, which indicated that 2 models had that predictor with a positive coefficient, whereas 1 model had it with a negative coefficient). Signs represent results from models with main effects only.

^cValues <0.001 are reported as 0.

3.2 *Marmots*

Christophersen (2012) counted 228 marmots during surveys in 2007-2008, and we counted 60 marmots in 2016 for analyses of relative abundance and weather predictors. Mean marmot abundance across sites decreased by 69% from 2007-2008 to 2016 ($\chi^2_1 = 86.1, p < 0.001, 95\%$ CI = 54, 84), and marmots were not detected at any station within 3 of 19 sites that were occupied in 2007-2008. Across sites, the percentage of 79 survey stations with marmot detections decreased from 70% in 2007-2008 to 37% in 2016. In 2016, marmots were detected at 6 of 24 stations without previous detection, but were not detected at 32 of 55 stations occupied in 2007-2008. Relative abundance of marmots did not increase from 2007-2008 to 2016 at any site (Figure 4), and losses were similar across elevations ($\chi^2_1 = 1.0, p = 0.312$). Despite correlation between snowpack duration and elevation, snowpack duration in 2015 explained more of the differences in marmot abundance over time than did elevation ($\chi^2_1 = 2.0, p = 0.156, \Delta AIC = 5.9$). The ratio of juvenile to subadult to adult marmots observed in 2016 (12:2:30) differed from that of 2007-2008 (32:32:145) and 2017 (22:6:57) with more juveniles but fewer subadults than expected in recent years ($\chi^2_4 = 35.2, p < 0.001$).

We counted 91 marmots in 2017, which was similar to the previous year and represented a 52% decrease from 2007-2008 ($\chi^2_1 = 113, p < 0.001, 95\%$ CI = 23, 81). In 2017, marmots were detected at 14 of 19 sites and at 43% of survey stations, of which, 4 stations did not have detections in 2007 or 2008. In 2017, we observed marmots at 18 stations that did not have detections in 2016, and did not detect marmots at 12 stations where they were present in 2016. The best model for marmots explained 88% of the conditional variation and 77% of the marginal variation in the relative abundances of marmots from 2016 to 2007-2008. This model included the interaction of chronic cold with maximum VPD in winter with a 1-year lag (Table

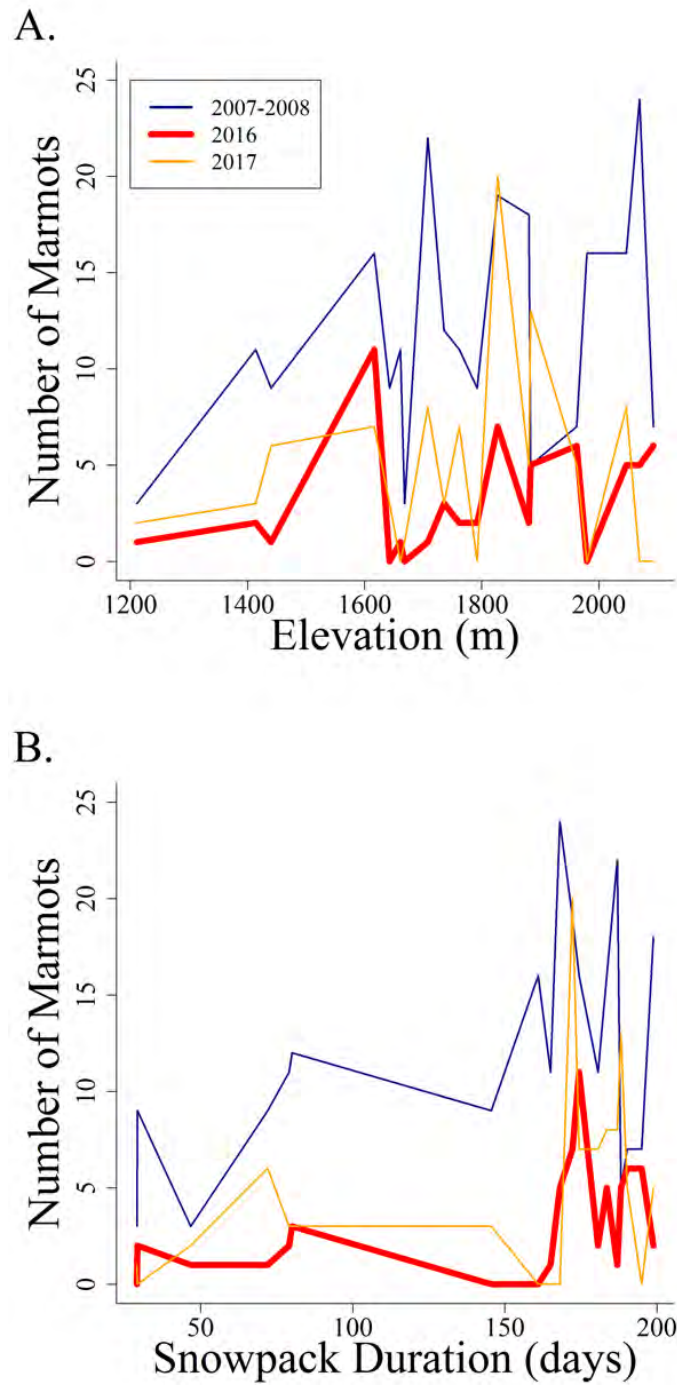


Figure 4. The number of hoary marmots with A) elevation and B) snowpack duration in 2015 at 19 sites that were surveyed in 2007-2008, 2016, and 2017 in North Cascades National Park, Washington, USA.

1). The second best model ($\Delta AIC_c = 2.3$) was the same as the best model for pikas, but the interaction of snowpack duration with minimum VPD during winter indicated that marmot abundances increased with moisture, rather than aridity. Models that represented winter weather or snowpack dynamics had Akaike weights that summed to >0.99 . Models that included winter VPD and its additive or interactive effects with cold exposure or snowpack formed most of the top-ranked models with a cumulative Akaike weight >0.97 . Losses of marmots from 2007-2008 to 2016 were greatest in sites that were warm and dry during winter (Figure 3B, Table A.3). The best model based on summer weather had $\Delta AIC_c = 16.3$ and Akaike weight <0.001 . Similar to pikas, the 1-year lag effect that was evident for marmots suggests that winter 2015 was influential.

Our analysis that included marmot counts in 2017 yielded top models similar to those of the analysis of counts for 2007-2016, based on the dominance of winter weather, time lags, and interactions between cold exposure and moisture. The top model was the interaction of chronic cold with winter VPD minimum with a 1-year lag. The second best model was competitive ($\Delta AIC_c = 1.3$) and included the interaction of chronic cold with winter VPD maximum with a 2-year lag for the 2017 abundances, which suggested strong influence of winter 2015.

3.3 Weather Anomalies

As measured by gridded climate values, the winter of 2015 was anomalous to other years during 2003 through 2016 at our sites based on snowpack and VPD, but not ambient cold exposure (Figure 5; Table A.4). Snowpack duration, April 1 SWE, and air moisture were at their lowest levels in winter 2015. Measures of chronic and acute cold suggest 2015 was the warmest or among the warmest winters during the study period. Cold exposure without snowpack was consistently more severe at low, rather than high elevations across years.

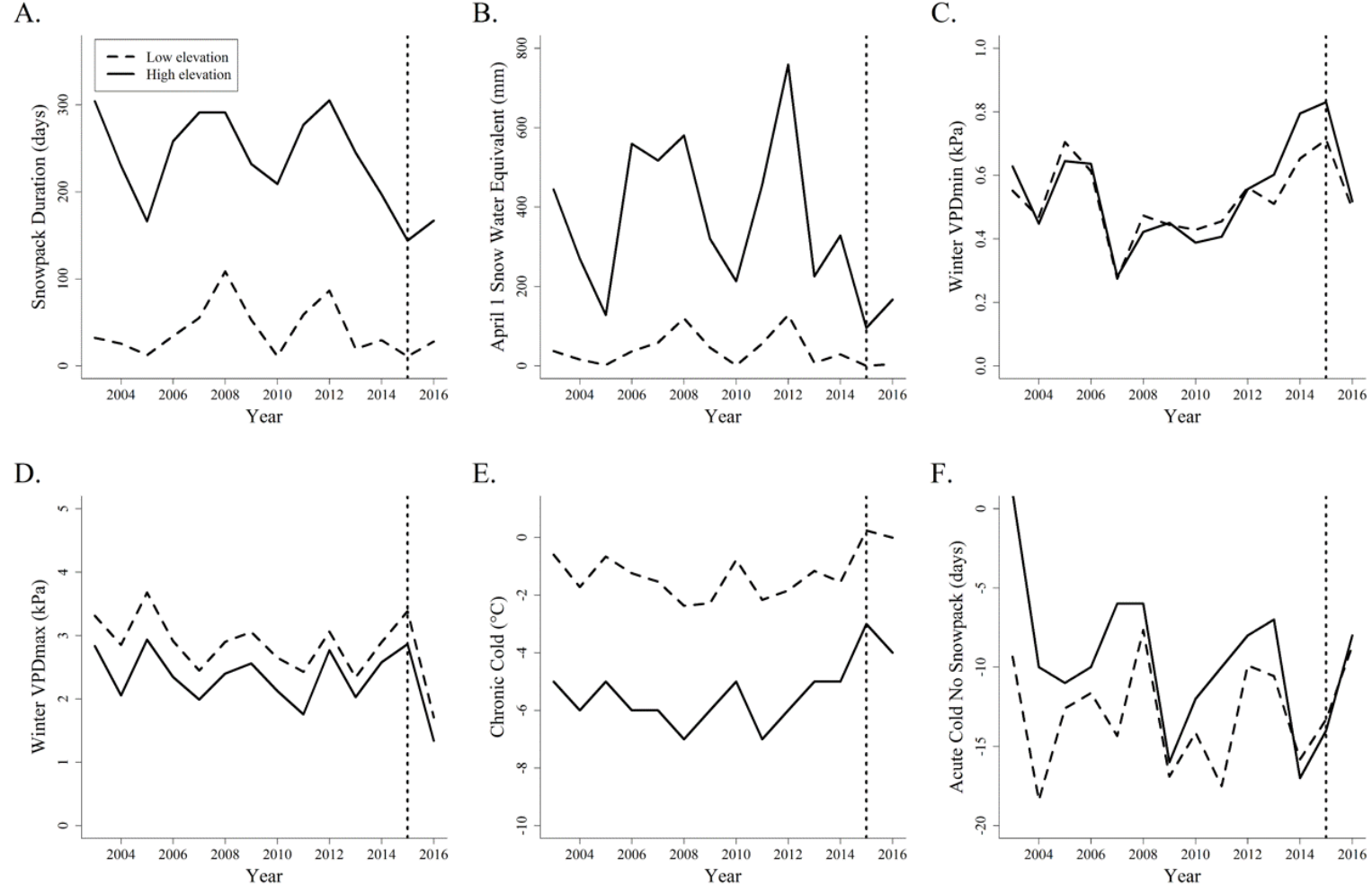


Figure 5. Snowpack duration (A), April 1 snow water equivalent [SWE] (B), winter VPD minimum (C), winter VPD maximum (D), chronic cold (E), and acute cold without snowpack (F) averaged for low- (<1400m) and high-elevation (>1400 m) sites from 2003-2016 at North Cascades National Park, WA, USA. The vertical dotted-line marks the record-low snowpack in 2015.

DISCUSSION

4.1 Winter weather and snowpack matter

Winter weather and snowpack dynamics profoundly affected abundances of pikas and marmots in North Cascades in surprising, unexpected ways. Our results demonstrate nuanced responses to weather and snowpack within and between species that are commonly ignored in analyses of species responses to climate change and conservation planning. First, the strong support for models with interactions between weather and snowpack dynamics indicate that context-dependent responses occur within mountain ranges. Our top model for pikas, for example, indicated that the influence of snowpack depended on moisture. Moreover, the response of pikas to the snowpack anomaly differed considerably between high and low elevations. Second, differential responses between two syntopic, climate-sensitive species to weather and snowpack have important implications for the use of indicator species for conservation planning. Although pikas and marmots shared associations with cold environments, the differences in their relation to moisture could lead to substantially different areas prioritized for conservation. Third, our top models for pikas and marmots, to our knowledge, are unprecedented in their application of VPD as a predictor of animal abundance. Moisture is an important aspect of climate that influences water stress on biota; however, few studies have used any metric of moisture to evaluate animal distributions [16]. The importance of VPD and its interaction with cold exposure or snowpack duration indicates that animals can respond strongly to moisture and that predictors of VPD may improve distribution models for other species. Our results suggest that continued warming, higher VPD, and further loss of snowpack [22,29,33,78] will be problematic for pikas and marmots [44,47] and may alter food webs to transform

montane ecosystems [31,79]. The ecological consequences of these changes to montane communities are intricate and complicate conservation strategies. Therefore, it is important to identify mechanisms that determine population dynamics to evaluate potential strategies for species conservation, such as managing for climate refugia [34].

4.2 *Winter versus summer weather*

Winter weather and snowpack dynamics explained significantly more variation in pika and marmot abundances than summer weather. Whereas most studies have implicated heat exposure as the mechanism of range retraction for *O. princeps* in the southern portion of its geographic range [43,80,81], but see Beever et al. [18], winter weather dynamics were resoundingly more important in North Cascades. In the Pacific Northwest, pikas occur at extraordinarily low elevations because of maritime effects and climate refugia that minimize exposure to high temperatures [82,83]. Persistent snowpack probably limits forage availability for pikas at high elevations in the North Cascades [84] because this region receives the highest annual snowfall in the world [85]. Like pikas, marmots are poorly adapted to heat exposure [44], yet, our models with heat exposure explained little variation in relative abundance of marmots. Similarly, winter weather strongly affects hoary marmots at the northern extent of their range in Canada [50]. There, early snowmelt reduces survival of hoary marmots, particularly among young marmots in hibernation, most likely via cold stress from lack of insulation [50,51]. Contrary to the common finding that range retractions associated with climate change occur primarily at the warm edges of species' ranges [5], our results suggest that species losses from climate change can occur elsewhere within cold regions with substantial snowpack.

4.3 Direct versus indirect mechanisms

Most of our evidence indicated that pikas and marmots were directly affected by winter weather and snowpack, contrary to more-common mechanisms of biotic interactions that arise from changing environmental conditions [25]. We constructed our top models for pikas and marmots to represent effects of physiological stress, and these models had overwhelmingly strong support over models that represented biotic interactions (e.g., growing-season precipitation). However, some results suggested that our top models could reflect biotic interactions. For example, snowpack was important to pikas, but our predictors for cold exposure without snowpack explained little variation in their relative abundances. Effects of cold exposure were consistent across alternative temperature thresholds for our metrics of cold exposure with and without snowpack, based on a *post-hoc* analysis (Appendix B). Furthermore, cold exposure in 2015 was similar in other years from 2003-2016 because winter was unusually warm in 2015 [32,33]. Also, the relative abundance of pikas shifted one year after the snowpack anomaly, indicating that mass mortality from freezing did not occur in winter 2015. This lag effect on pika abundances at low elevations could be explained by stress-induced fetal resorption from cold exposure in the absence of snowpack [86] or malnutrition from poor plant productivity [84,87]. Reduced water availability for plants and early senescence could have hampered haypile construction in 2015 and led to starvation in the following winter. At high elevations, earlier snowmelt may have increased reproduction and overwinter survival of pikas in 2015 because of the increase in season length for plant availability to an optimal duration. Similar lag effects of snowpack on survival rates, but not reproduction, of collared pikas (*Ochotona collaris*) were attributed to forage availability in Canada [84]. The influence of direct and indirect effects of climate change may be context-dependent and not mutually exclusive. Conditions could have

been physiologically stressful for pikas at low elevations, while earlier snowmelt at high elevations could have lengthened the period of forage availability. To examine these alternative explanations, we conducted a *post-hoc* analysis of pika and marmot counts with metrics of vegetative phenology and productivity from time series of the normalized difference vegetation index (NDVI) in imagery from the Moderate Resolution Imaging Spectroradiometer (MODIS; [88]; Appendix B). Our models of vegetative phenology and productivity were not competitive with our top *a priori* model for pikas, but they did explain significant variation in abundances and effects were consistent with our hypotheses about biotic interactions. Therefore, both physiological stress during winter and forage availability likely affected pikas, but physiological stress was the strongest factor.

Physiological stress from weather more likely affected marmots than biological interactions. Marmots may have been stressed during hibernation from exposure to cold, dry air [89,90,91]. Extreme cold may not be necessary to reduce marmot fitness because differences in energy expenditure of hibernating marmots are significant when ambient temperatures are 5 versus 0°C [89]. Although, the frequency of these temperatures without snowpack in 2015 was similar to other years, the combination of cold temperatures with dry air was unusual. Subnivean air moisture is high and decoupled from surface conditions because of snow cover [92,93]. Consequently, the short duration of snowpack in 2015 may have increased exposure to cold, dry conditions for marmots while they were still hibernating and inflicted physiological stress through dehydration and cold exposure. Patterns in metabolic rates of yellow-bellied marmots (*Marmota flaviventris*) show a) increased stress in warm, dry habitats, and b) local adaptation to water loss and thermoregulation [94]. Alternatively, exposure to unstable temperatures in burrows during snow-free conditions may have triggered early emergence of marmots from

hibernation [50]. Energy expenditure of euthermic marmots is significantly higher than hibernating marmots [94,95], and temperature influences timing of emergence. Whether early emergence is beneficial for hoary marmots probably depends on forage availability at the time of emergence. Early snowmelt and dry air may reduce the quality and quantity of forage for marmots [30,96,97,98], but results of our analyses with vegetative phenology and productivity provided relatively little support for mechanisms related to biotic interactions.

Like pikas, hoary marmots have also shown 1-year lag effects from low snowpack on adult survival [50]. Because our counts of subadult marmots were less than expected in 2016 and 2017, fetal resorption or low overwinter survival of juveniles are plausible explanations for marmot losses [50,87,91]. Our results indicate that winter conditions in years of snow drought negatively affect marmots, but some anecdotal reports of marmot losses in the Park preceded the low snow year. Because our data for marmots was limited to two time-periods, it remains unclear whether the majority of marmot losses occurred abruptly in 2015 or gradually since 2007 due to longer-term changes in weather and snowpack.

4.4 Hibernating versus hoarding

Our top models for pikas and marmots were remarkably similar in the weather factors that were important, as indicated by the interaction of moisture and snowpack duration (pikas) or cold exposure (marmots). However, marmots favored cold, moist sites, whereas relative abundance of pikas was highest at cold, dry sites. Furthermore, marmots appeared more sensitive to cold exposure without snowpack than pikas. Differences between pikas and marmots in their winter coping strategies, niche, and geographic distribution may explain their sensitivities to moisture and temperature [50,99]. Unusually dry air and short snowpack duration could have

stressed hibernating marmots, but pikas are active throughout winter and may mitigate stresses by 1) moving into microrefugia (e.g., beneath snow drifts, deep talus) to avoid cold exposure or 2) drinking water as needed [16]. Talus matrices used by pikas have thermal dynamics [100] that may provide better insulation from cold than burrows without snow cover. Although marmots conserve warmth by hibernating socially, these benefits can be overwhelmed by extreme cold [52,91]. Furthermore, pikas may survive on forage with lower water content than marmots because of the reliance on haypiles by pikas rather than fat for winter survival [101]. The sensitivity of hoary marmots to dryness and temperature in the Park may reflect their position at the southern edge of the species' geographic range, which extends to the central Alaska in cold, mesic mountain ranges. Marmots may inhabit dryer climates further east, but these sites are colder, and physiological adaptations to moisture and temperature can vary within marmot species [94]. In contrast, the geographic range for pikas covers extensive regions at lower latitudes in warmer, drier portions of North America.

The near universal increase in relative abundance of pikas at high elevations after winter 2015 is a striking contrast with the marmot response. Pikas inhabit a broader range of elevations than marmots in North Cascades and were distributed such that peak densities occurred at intermediate elevations prior to the low-snow year. This peak appeared to shift upwards in elevation after winter of 2015, consistent with the hypothesis (Fig 1) that habitat suitability for alpine species will move up in elevation with climate change [102]. In contrast, marmots occupy a relatively narrow range of elevations and may not be able to move higher in the Park.

4.5 *Alternative mechanisms*

Our weather-based predictors explained much variation in the change in relative abundances of pikas and marmots, but other mechanisms may contribute to a smaller portion of the variability we observed. For example, recent losses of Olympic (*Marmota olympus*) and Vancouver Island (*M. vancouverensis*) marmots were attributed to predation by coyotes (*Canis latrans*; [103], rather than weather. Bryant and Page [104] found high winter survival of Vancouver Island marmots but severe predation by cougars (*Puma concolor*) and wolves (*Canis lupus*) in late summer. Coyotes, wolverines (*Gulo gulo*), cougars, and other predators of marmots occur in the Park and may have contributed to marmot declines. Like predation, the influence of disease on hoary marmots is poorly understood. Diseases like tularemia are major sources of mortality for other sciurids in Washington and can be difficult to detect without intensive monitoring [105]. Nevertheless, the high explanatory power of our weather-based models and their consistencies with weather relationships described from long-term demographic and laboratory studies indicate that winter weather can exert strong influence on populations of pikas and marmots in the Park.

4.6 *Conclusions*

Winter weather and snowpack dynamics strongly affected pika and marmot populations in the Park. The ecological effects of declining snowpack under climate change pose a myriad of ecological challenges to animals and managers responsible for species conservation in montane ecosystems. Our results demonstrate the nuanced and context-dependent responses of pikas and marmots to weather and snowpack dynamics that likely occur in other species. This variability within and among species needs to be understood to improve forecasts of species responses to

climate change. Predictors in many species distribution models are too simplistic to capture the interactive effects of temperature, precipitation, moisture, and snowpack that influence animals. Extreme weather can change animal abundances quickly, especially when limits of physiological tolerance are reached or biotic interactions become unfavorable. Mechanistic modeling approaches are needed to understand biotic responses to climate change and inform conservation strategies. Climate predictions of increasing temperatures and aridity do not favor some alpine species, and losses to extreme weather can be rapid.

MANAGEMENT IMPLICATIONS

American pikas and hoary marmots are members of the wildlife community in North Cascades that is recognized as a fundamental resource by the National Park Service [106]. Fundamental resources, such as high-elevation meadows and old-growth forests, are prioritized for management because of their important role in meeting the mission of the National Park Service. Pikas are considered Species of Greatest Conservation Need (SGCN) in 8 of the 10 U.S. states in which they occur, including Washington [107]. The SGCN list informs the State Wildlife Action Plan and is intended to notify managing agencies of the need for voluntary conservation actions for vulnerable species. Pikas are listed as SGCN in Washington because of their vulnerability to climate change. Hoary marmots are not SGCN in Washington, but are listed as SGCN in Idaho and have been recognized, along with pikas, as an indicator species for climate change and a Species of Greatest Inventory Need in Montana [108,109,110].

More broadly, pikas and marmots are considered species of least concern in the International Union for Conservation of Nature (IUCN) Red List because they are common and widespread throughout much of their geographic range [111,112]. The IUCN recognizes that

pika populations are in decline due to climate change, whereas marmot populations are considered stable with no major threats. Listing of American pikas for protection under the Endangered Species Act was found unwarranted in 2010 and 2016 because declines were documented primarily in the Great Basin and did not meet the severity criteria for protection [113,114,115]. It is unlikely that these species will receive elevated status for protection in the near future, even if populations continue to decline in North Cascades. Consequently, losses of pikas and marmots within North Cascades may not generate the level of support for research and recovery efforts, as seen for species with elevated legal protections.

American pikas and hoary marmots have been proposed as indicator species for the effects of climate change in mountain ecosystems [65,102,116,117]. Our results indicate that winter weather and snowpack dynamics significantly affect populations of pikas and marmots in North Cascades. Forecasts of increasing temperatures and aridity under climate change do not favor these species [22,78,118]. Snowpack has already declined at many localities in the Pacific Northwest by more than 40% over the past century [57]. Rising temperatures are expected to continue this trend despite expected increases in precipitation. Our models suggest that further reductions in snowpack will negatively affect pika populations at low elevations in the near term. Positive effects of reduced snowpack on pikas at high elevations observed in this study suggest that pikas might persist at high elevations in North Cascades for considerable time, but these effects may dissipate, if snowpack continues to decline.

Our models also suggest that rising temperatures and increasing aridity will be detrimental for marmots. Ficklin and Novick [78] estimate a 51% increase in summer VPD within the continental United States for the time period of 2065-2099 relative to values observed in 1979-2013. The widespread and precipitous decline of marmots in North Cascades revealed in this

study raises the possibility that management actions to prevent further losses or recover the species might be needed in the near term. However, considerable knowledge gaps about marmot population dynamics and distribution within North Cascades obscure the need for immediate action. Because our assessment for marmots is based on abundances from only two time periods (2007-2008 and 2016-2017), some uncertainty remains about population status and capacity for recovery. Our 19 sites for marmot surveys covered an unknown fraction of the population within the Park because habitat amount, distribution, and occupancy have not been fully inventoried across the Park's entire area. In addition, there is much uncertainty about whether marmot losses at North Cascades occurred in other regions because research on population dynamics has been extremely limited for hoary marmots [50]. Significant questions that remain to more definitively assess vulnerability include:

- 1) Is the 69% decline in marmot abundances that we observed 1) within the range of natural interannual population fluctuation, 2) part of a persistent decline, or 3) indicative of a new dynamic range?
- 2) Will pikas and marmots recover in the absence of further weather anomalies?
- 3) What is the contribution of predation and disease to the declines that we observed?
- 4) If climate change is detrimental to pikas and marmots, are there climate refugia in the North Cascades?
- 5) How will temperature, moisture, and snowpack vary in the future at various spatial resolutions?

The most important action needed to inform management in the near term is to monitor marmots and pikas [48,61] to document recovery or patterns of loss over the next several years and to conduct research that further quantifies the contribution of direct (e.g., physiological stress

from temperature extremes, predation) and indirect (e.g., forage availability) mechanisms that drive population dynamics. Follow-up investigations that would be useful to inform managers of risk and the need for specific actions for pikas and marmots include studies of predator-prey dynamics, disease, and field-based mechanistic research on micro-climate, physiological stress, and forage responses to weather and snowpack dynamics. If climate change is a significant phenomenon affecting pikas and marmots, extending research to other alpine species (e.g., ptarmigans, butterflies, golden-mantled ground squirrels, vegetation) is needed to assess community changes under climate change that ultimately may lead NPS to revise management objectives.

Bruggeman [48] assessed pika population dynamics in North Cascades and recommended continued monitoring of pikas in favor of management actions of 1) habitat protection, 2) habitat creation, and 3) translocation. Each of these strategies is also applicable to marmots. The National Park Service affords considerable habitat protection in North Cascades through wilderness designation. Additional protections could include focused efforts to suppress fire around important habitats for these species. Protections also could be provided by diverting human activities away from habitats with pikas or marmots. However, Bruggeman [48] and others [112] have not detected consequences of human activities around pika habitats, and pikas are abundant along popular hiking trails in North Cascades. Likewise, we observed marmots in high abundance along popular trails including Cascade Pass and Hannegan Pass. We also observed marmots along the highway near Rainy Pass, where “wildlife crossing” signs might be useful for reducing animals being struck by automobiles. Our presence occasionally disrupted the foraging of marmots, but it is unknown whether regular interruptions by hikers translate to

fitness consequences for *M. caligata*. Studies of marmot-human interactions may be useful to evaluate the utility of diverting human activities as a management strategy for marmots.

Habitat creation is possible for pikas because they readily inhabit rock piles created by humans that resemble talus [82,119]. Marmots often share habitat with pikas in talus and may respond to man-made habitats. However, such strategies are likely prohibitively expensive to employ except in highly strategic locations, accessible by road. Strategic applications may seek to increase connectivity between important source populations. Such actions could be warranted if populations become critically low, but cost-benefit analyses that includes alternative strategies would be informative. Similarly, animal translocations are usually implemented to reintroduce a species or augment a critically low population [117]. If translocation becomes a viable management option for pikas or marmots, issues concerning logistics, disease, and genetics need careful consideration for successful implementation [120]. If climate change is underlying population declines, locating sites for translocation or habitat creation could be especially challenging because habitats that were suitable in the recent past may no longer support these species. Identification of climate refugia and their resistance to climate change could help assess risk and manage populations of pikas and marmots imperiled by climate change.

Climate refugia support species persistence during times of inhospitable environmental conditions, and identifying such refugia is important for species conservation as climate changes [34,121]. Occurring across a range of spatial and temporal scales, refugia function in different and important ways, allowing species to cope with changing environments. At broader scales, coastal areas such as the Olympic Peninsula, for example, have maintained mild climates even during ice ages when interior areas were covered by glaciers [122]. Species like Douglas-fir (*Pseudotsuga menziesii*) persisted within these lowland refugia and quickly colonized interior

regions as glaciers retreated [123]. At moderate scales, local physiography can concentrate cool air pooling into areas like valley bottoms that can alter moisture regimes and support unique biota [121]. At the finest scales, air temperatures within talus matrices can be $>30^{\circ}\text{C}$ cooler than on the nearby surface; these matrices provide refuge from extreme heat for species such as the American pika [83]. Broad- or moderate-scale refugia can be identified with widely available climate surfaces such as PRISM [121,124], which were used in our analysis. Data from this project can be used to map habitat suitability and identify climate refugia to provide useful tools to aid decision-making. Our models provide an index of habitat suitability for pikas and marmots based on temperature, moisture, and snowpack predictors that can be mapped and forecasted based on climate scenarios to assess resistance of climate refugia over time. These models can incorporate physical habitat features (e.g., talus, vegetation) to create maps that provide spatially-explicit information on the amount and distribution of habitat for pikas and marmots to prioritize conservation planning.

In conclusion, continued monitoring and research to identify mechanisms that govern population dynamics of pikas and marmots are important to determine the need and strategies for management actions. Significant reductions in marmot abundances and distribution in the Park between 2007 and 2016 illustrate the potential of common species quickly becoming uncommon under climate change. Reversing climate change, of course, is far beyond the reach of local managers, but, as educators, NPS could inform visitors on the state of our knowledge on the consequences of climate change. Finally, synthesis of pika and marmot responses to weather and snowpack dynamics with the responses of other alpine species could provide a more comprehensive assessment of resource risk for North Cascades and facilitate development of new tools to aid managers.

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APPENDIX A.

Table A.1. Weather and snowpack predictors in the analyses of relative abundances of American pikas and hoary marmots from 2007-2016 in Washington, USA.

	Unit	Definition
Chronic heat	°C	mean daily maximum temperatures for July-August
Acute heat	days	number of days with temperature >25°C
Growing-season precipitation	mm	sum of daily precipitation for July-September
Vapor pressure deficit minimum	kPa	mean daily minimum VPD for June-September, or November-February
Vapor pressure deficit maximum	kPa	mean daily maximum VPD for June-September, or November-February
Chronic cold	°C	mean daily minimum temperature for November-February
Acute cold	days	number of days with temperature <-10°C for September-August
Chronic cold without snowpack	days	number of days with temperature <0°C and SWE<30mm for September-August
Acute cold without snowpack	°C	minimum temperature while SWE<30mm for September-August
Snowpack duration	days	number days with SWE>30mm for September-August

Table A.2. *A priori* models for the analyses of relative abundances of American pikas and hoary marmots in North Cascades National Park, USA, 2007-2016.

Model ^a	Model
1. Summer VPDmax+Growing-Season Precipitation	24. Chronic Cold without Snowpack
2. Summer VPDmin+Acute Heat+Growing-Season Precipitation	25. Winter VPDmin
3. Summer VPDmin+Chronic Heat+Growing-Season Precipitation	26. Winter VPDmax
4. Summer VPDmin*Acute Heat	27. Acute Cold+Winter VPDmax
5. Summer VPDmin*Chronic Heat	28. Acute Cold+Winter VPDmin
6. Growing-Season Precipitation*Acute Heat	29. Acute Cold*Winter VPDmax
7. Growing-Season Precipitation*Chronic Heat	30. Acute Cold*Winter VPDmin
8. Growing-Season Precipitation+Acute Heat	31. Chronic Cold+Winter VPDmax
9. Growing-Season Precipitation+Chronic Heat	32. Chronic Cold+Winter VPDmin
10. Growing-Season Precipitation	33. Chronic Cold*Winter VPDmax
11. Acute Heat	34. Chronic Cold*Winter VPDmin
12. Chronic Heat	35. Acute Cold without Snowpack*Winter VPDmax
13. Summer VPDmin	36. Acute Cold without Snowpack+Winter VPDmax
14. Summer VPDmax	37. Chronic Cold without Snowpack*Winter VPDmax
15. Acute Cold	38. Chronic Cold without Snowpack+Winter VPDmax
16. Acute Cold+Acute Cold without Snowpack	39. Acute Cold without Snowpack*Winter VPDmin
17. Acute Cold+Chronic Cold without Snowpack	40. Acute Cold without Snowpack+Winter VPDmin
18. Chronic Cold	41. Chronic Cold without Snowpack*Winter VPDmin
19. Chronic Cold+Acute Cold without Snowpack	42. Chronic Cold without Snowpack+Winter VPDmin
20. Chronic Cold+Chronic Cold without Snowpack	43. Snowpack Duration+Winter VPDmax
21. Snowpack Duration+Snowpack Duration ²	44. Snowpack Duration+Winter VPDmin
22. Snowpack Duration	45. Snowpack Duration*Winter VPDmax
23. Acute Cold without Snowpack	46. Snowpack Duration*Winter VPDmin

^aFor pikas, predictors represented values from the year of each survey. In addition, we tested this model set with a 1-year time lag such that predictors that represented conditions from the previous year. Together, there were 93 candidate models for the analyses of pikas, including the null model. For marmots, predictors represented averaged values from 2003-2016. As additional candidate models, we substituted the snowpack duration of winter 2015 for all models above that included Snowpack Duration. The total number of candidate models for marmots was 53, including the null model.

Table A.3. Effect estimates from univariate models for predictors in the analysis of relative abundances of American pikas and hoary marmots in North Cascades National Park, Washington, USA, 2007-2016.

Predictor ^a	Season	<u>Pika</u>		<u>Marmot</u>	
		β	SE	β	SE
Acute heat (days)	Summer	-0.234	0.137	-0.649*	0.092
Chronic heat (°C)	Summer	-0.116	0.146	-0.254*	0.093
Growing-season precipitation (mm)	Summer	0.104*	0.048	-0.831*	0.094
Min vapor pressure deficit (kPa)	Summer	0.0636	0.0437	-0.353*	0.072
Max vapor pressure deficit (kPa)	Summer	-0.123	0.115	0.175	0.111
Acute cold (days)	Winter	-0.121	0.063	0.561*	0.066
Chronic cold (°C)	Winter	-0.0881	0.101	-0.719*	0.076
Acute cold without snowpack (°C)	Winter	0.0670	0.0540	0.430*	0.065
Chronic cold without snowpack (days)	Winter	-0.0776	0.0606	-0.476*	0.103
Snowpack duration (days)	Winter	0.153	0.094	0.793*	0.083
Min vapor pressure deficit (kPa)	Winter	0.0853	0.0510	-0.600*	0.093
Max vapor pressure deficit (kPa)	Winter	0.0355	0.0549	-0.707*	0.107

^aAll predictors were standardized to a normal distribution with a mean of 0 and standard deviation of 1 for the analysis. Estimates are for 1-year lag effects.

* $P < 0.05$

Table A.4. Results of mixed-effects models (β , SE, F) that compared weather and snowpack in 2015 with and other years from 2003-2016, and rank of 2015 versus other years at low (<1,400 m) and high (>1,400 m) elevation sites, where highest ranking years had the least snowpack (April 1 SWE, snowpack duration), highest vapor pressure deficit (VPD), and the most severe cold exposure in North Cascades National Park, WA, USA.

	β	SE	F	Rank Low Elevation	Rank High Elevation
Snowpack Duration (days)	-73.3	8.2	81	1	1
April 1 SWE (mm)	-190	25	55	1	1
Winter VPDmin (kPa)	0.266	0.021	155	1	1
Winter VPDmax (kPa)	0.586	0.076	59	2	2
Chronic Cold (°C)	2.14	0.13	287	14	14
Acute Cold (days)	-8.10	1.29	39	10	13
Chronic Cold without snowpack (days)	-1.96	3.99	-0.24	12	5
Acute Cold without snowpack (°C)	-2.84	0.86	11	7	3

APPENDIX B. Methods and results of *post-hoc* analyses of relative abundances of American pikas and hoary marmots in North Cascades National Park, WA, 2007-2016.

B.1 Methods

We conducted *post-hoc* analyses to investigate further 1) the hypothesis that exposure to cold without snowpack negatively affects pikas and marmots, and 2) the influence of biotic interactions. We tested effects of cold exposure with and without snowpack measured as the number days below alternative temperature thresholds of 0, -5, and -10°C. Because these predictors explained little variation in relative abundance of mammals without accounting for moisture, we included the interaction of minimum VPD during winter with each predictor of cold exposure in alternative models.

We tested a *post-hoc* model set (Table B.1) to discriminate direct (i.e., physiological stress) and indirect effects (i.e. forage availability) of weather and snowpack that were implied by our top models in our analyses of weather and snowpack dynamics. Predictors were derived from time series of the normalized difference vegetation index (NDVI) in imagery from the Moderate Resolution Imaging Spectroradiometer (MODIS) aboard the Terra satellite [88]. We used measures of phenology (start of season, end of season, season duration) and productivity (cumulative NDVI, maximum NDVI, NDVI amplitude) that were calculated from the NDVI curve for each year of the study period. These metrics were calculated by the U.S. Geological Survey and were available at (<https://doi.org/10.5066/F7PC30G1>, accessed 31 January 2018). Smoothing for NDVI curves followed a moving-window approach with regressions of the NDVI values. Models represented hypotheses about the effects of vegetative phenology and productivity on abundances of pikas and marmots. We expected that abundances would increase with forage availability, which should increase with growing-season duration and productivity. Early senescence, however, should limit forage availability during a critical period when pikas

Table B.1. *Post-hoc* set of models with predictors that represented plant phenology or productivity for the analyses of relative abundances of American pikas and hoary marmots in North Cascades National Park, USA, 2007-2016.

Model ^a	Model
1. Start of Season	16. Cumulative NDVI * VPDmax
2. Start of Season + Start of Season ²	17. Maximum NDVI
3. End of Season	18. Maximum NDVI * Start of Season
4. Season Duration	19. Maximum NDVI * Season Duration
5. Start of Season * VPDmin	20. Maximum NDVI * End of Season
6. End of Season * VPDmin	21. Maximum NDVI * VPDmin
7. Season Duration * VPDmin	22. Maximum NDVI * VPDmax
8. Start of Season * VPDmax	23. Maximum NDVI + Cumulative NDVI
9. End of Season * VPDmax	24. NDVI Amplitude
10. Season Duration * VPDmax	25. NDVI Amplitude * Start of Season
11. Cumulative NDVI	26. NDVI Amplitude * Season Duration
12. Cumulative NDVI * Start of Season	27. NDVI Amplitude * End of Season
13. Cumulative NDVI * Season Duration	28. NDVI Amplitude * VPDmin
14. Cumulative NDVI * End of Season	29. NDVI Amplitude * VPDmax
15. Cumulative NDVI * VPDmin	

^aPredictors represented conditions from the previous year. Minimum vapor pressure deficit = VPDmin. Maximum vapor pressure deficit = VPDmax.

build haypiles or marmots accumulate fat for winter survival. Because of strong evidence for the effects of moisture on abundances of pikas and marmots in the *a priori* analysis, we included models with the interactions between VPD and metrics of phenology or productivity. For example, the effect of season duration may depend on the moisture, because moisture can increase plant productivity and ultimately, the marginal energy acquired in bouts of foraging. Predictors represented conditions from the summer prior to each year's survey because results of the *a priori* analysis indicated that weather had 1-year lag effects on pikas and marmots. We also tested for differences in phenology and productivity in 2015 from other years from 2003-2016 with linear mixed-effects models.

B.2 Results

Results of the *post-hoc* assessment of cold exposure with and without snowpack at varying temperature thresholds for pikas were mixed (Table B.2). However, the model set that included winter VPD minimum was much stronger, and the predictor of cold exposure, ignoring snowpack presence, based on a 0°C threshold and a 1-year lag effect was clearly best. There was little support for negative effects of cold exposure without snowpack based on univariate models. For marmots, predictors of cold exposure explained more variation in marmot counts than those that measured cold exposure without snowpack ($\Delta AICc > 29$). However, significantly negative relationships between marmots and cold exposure without snowpack were evident and contrasted with the significantly positive relationships with our measure of cold exposure that ignored the presence of snowpack. Although models with cold exposure in the absence of snowpack had relatively high AIC values, these results corroborate effects observed in the *a priori* analysis (Tables 2, A.3) and indicate that cold exposure without snowpack negatively affected marmots.

Table B.2. *Post-hoc* analyses of cold exposure, measured as the number of days with temperatures below a threshold including (snow = yes) and excluding (snow = no) days with snowpack in the analysis of relative abundances of American pikas and hoary marmots in North Cascades National Park, WA, USA, 2007-2016.

Threshold	Snow	Species	Period ^a	β^b	SE	ΔAIC_c	Interaction ^c ΔAIC_c
0 °C	yes	pika	current	0.247	0.159	15.9	15.6
0 °C	no	pika	current	0.072	0.067	16.6	15.9
5 °C	yes	pika	current	0.007	0.118	17.8	16.4
5 °C	no	pika	current	0.017	0.063	17.7	18.4
10 °C	yes	pika	current	-0.101	0.055	14.7	15.2
10 °C	no	pika	current	-0.016	0.057	17.7	18.4
0 °C	yes	pika	lag	0.142	0.103	16.0	0
0 °C	no	pika	lag	-0.078	0.061	16.2	17.0
5 °C	yes	pika	lag	-0.033	0.084	17.6	10.5
5 °C	no	pika	lag	-0.050	0.060	17.1	18.3
10 °C	yes	pika	lag	-0.121	0.063	14.6	14.6
10 °C	no	pika	lag	-0.026	0.053	17.5	18.5
Null		pika				15.6	
0 °C	yes	marmot	current	0.714*	0.090	37.5	17.4
0 °C	no	marmot	current	-0.619*	0.117	81.1	29.4
5 °C	yes	marmot	current	0.691*	0.097	49.6	18.3
5 °C	no	marmot	current	-0.034	0.082	119	49.7
10 °C	yes	marmot	current	0.549*	0.072	50.2	31.0
10 °C	no	marmot	current	0.258*	0.069	105	44.7
0 °C	yes	marmot	lag	0.757*	0.079	8.83	0
0 °C	no	marmot	lag	-0.476*	0.103	94.8	61.9
5 °C	yes	marmot	lag	0.703*	0.074	12.1	0.062
5 °C	no	marmot	lag	-0.414*	0.086	94.5	56.6
10 °C	yes	marmot	lag	0.562*	0.066	40.8	19.9
10 °C	no	marmot	lag	-0.590*	0.077	52.4	42.3
Null		marmot	lag			117	

^aMeasures of cold exposure were from the winter prior (current) or 1 year previous (lag) to the pika or marmot survey.

^bEffect estimates are from univariate models.

^cModel comparisons for the set that included the interaction of cold exposure and minimum (pika) or maximum (marmot) vapor pressure deficit in winter in all models.

* $P < 0.05$

The best model for pikas that was based on phenology or productivity of vegetation explained 82% of the conditional variation and 18% of the marginal variation in pika counts but did not compete with the best model from the *a priori* analysis (Table B.3, $\Delta\text{AIC}_c = 6.0$). This model indicated that relative abundance of pikas increased with vegetative productivity at dry sites, but pika abundance changed little with productivity at moist sites (Figure B.1). The best model for marmots that was based on vegetation explained 89% of the conditional variation and 65% of the marginal variation in marmot counts but did not compete with the best model from the *a priori* analysis (Table B.3, $\Delta\text{AIC}_c = 23.3$, Akaike weight <0.001). The best vegetation-based model indicated that marmot abundances increased with productivity when the start of the growing season was late, but not when the season started early (Figure B.1). Results of univariate analyses (Table B.4) provided mixed support for our *post-hoc* hypotheses about the importance of forage availability and quality to marmots. For example, marmot abundances increased after years with a late season end but decreased after years with long growing seasons. Vegetative productivity based on cumulative NDVI was highest and the start of season was earliest in 2015 compared to other years (Table B.5, Figure B.2).

Table B.3. Top models with predictors based on plant phenology or productivity relative to the best and null models in the analyses of relative abundances of American pikas and hoary marmots in North Cascades National Park, WA, USA, 2007-2016.

Model ^a	Species	ΔAIC_c	w_i	R^2_c	R^2_m
Summer VPDmin * NDVI Amplitude	Pika	5.99	0.032	0.82	0.18
Summer VPDmax * NDVI Amplitude	Pika	7.14	0.018	0.81	0.21
NDVI Amplitude	Pika	10.3	0.004	0.79	0.15
Null	Pika	14.1	<0.001	0.83	0
Cumulative NDVI * Start of Season	Marmot	23.3	<0.001	0.89	0.65
Summer VPDmin * Start of Season	Marmot	25.4	<0.001	0.89	0.53
Start of Season	Marmot	26.2	<0.001	0.89	0.53
Null	Marmot	119	<0.001	0.57	0

^aMinimum vapor pressure deficit = VPDmin. Maximum vapor pressure deficit = VPDmax.

Predictors represented the year prior to the pika or marmot survey (1-year time lag). Models with interactions included main effects for each interacting predictor.

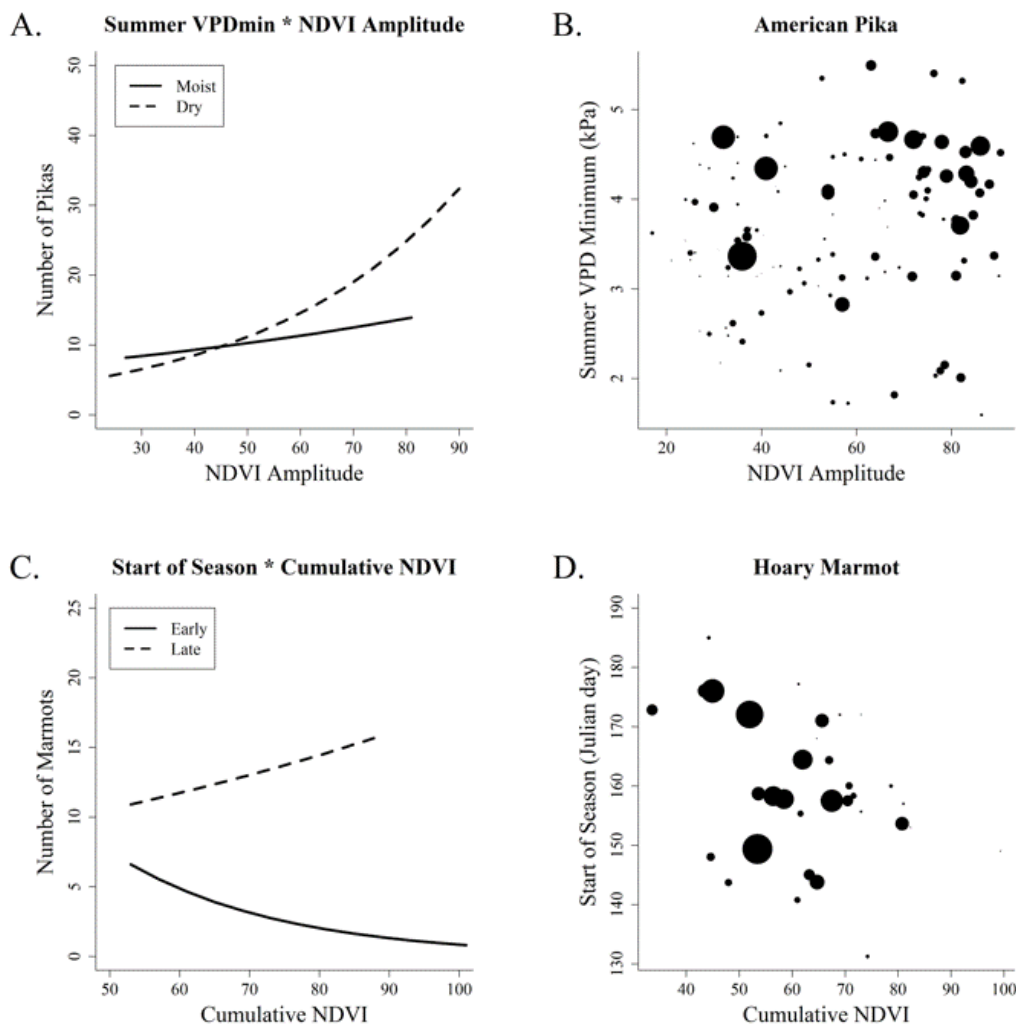


Figure B.1. Predicted values from the A) best model for relative abundance of American pikas based on vegetative phenology and productivity, as explained by the interaction of summer vapor pressure deficit minimum and NDVI amplitude; B) the relative density of pikas with summer VPD minimum and NDVI amplitude; C) the best model for relative abundance of hoary marmots, as explained by the interaction of the start of season and cumulative NDVI; and D) the relative abundance of marmots with the start of season and cumulative NDVI in the analyses of relative abundances for pikas and marmots at North Cascades National Park, Washington, USA, 2007-2016. Mean intercepts for the random sites were used for each prediction of pika density. Moist and dry prediction lines are based on the upper and lower 90th percentile values of winter VPD minimum observed within each dataset. Predictions cover the approximate range of values for the combination of VPD and snowpack or chronic cold observed in the datasets. Size of points in B and D increase with relative abundance of pikas or marmots. We calculated the relative density of pikas as the number of pikas counted at each site in each year divided the by the area of talus at each site.

Table B.4. Effect estimates from univariate models with predictors of vegetative phenology and productivity and the mean Akaike weight (\bar{w}_i) for each model with these predictors based on weights from the combined *a priori* and *post-hoc* model sets in the analysis of relative abundances of American pikas and hoary marmots in North Cascades National Park, Washington, USA, 2007-2016.

Predictor	Pika			Marmot		
	β	SE	\bar{w}_i	β	SE	\bar{w}_i
Start of season (Julian day)	0.0820	0.0847	<0.001	0.803*	0.093	<0.001
End of season (Julian day)	0.0167	0.0566	<0.001	0.159*	0.0717	<0.001
Season duration (days)	-0.0425	0.0732	<0.001	-0.657*	0.087	<0.001
Cumulative NDVI	0.189*	0.088	0.002	-0.689*	0.120	<0.001
Maximum NDVI	-0.0732	0.0687	<0.002	-0.293*	0.131	<0.001
NDVI amplitude	0.397*	0.147	0.009	0.024	0.111	<0.001

* $P < 0.05$

Table B.5. Results of mixed-effects models (β , SE, F) that compared vegetative phenology and productivity in 2015 with and other years from 2003-2016, and rank of 2015 versus other years at low (<1,400 m) and high (>1,400 m) elevation sites, where highest ranking years had the greatest shift in phenology (earliest start of season, earliest end of season, longest season duration) and highest productivity in North Cascades National Park, WA, USA.

	β	SE	F	Rank Low Elevation	Rank High Elevation
Start of season (Julian day)	-23.1	2.7	75.8	1	1
End of season (Julian day)	-1.01	2.52	0.16	3	7
Season duration (days)	22.1	3.7	36.5	3	1
Cumulative NDVI	15.2	2.0	60.7	2	1
Maximum NDVI	1.98	0.95	4.35	6	3
NDVI amplitude	-0.91	1.01	0.82	11	9

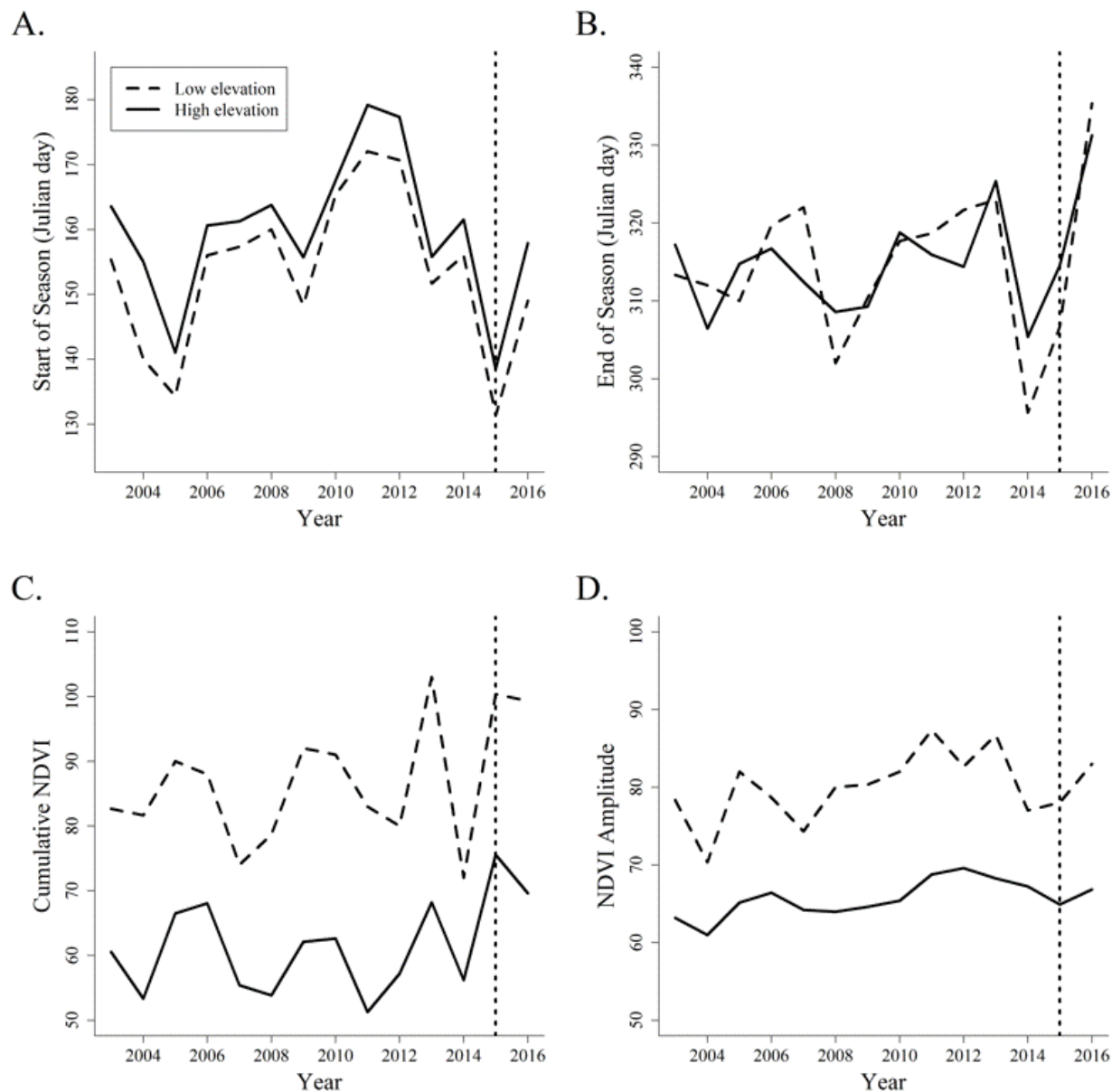


Figure B.2. Start of season (A), end of season (B), cumulative NDVI (C), and NDVI amplitude (D) at low- (<1400m) and high-elevation (>1400 m) sites from 2003-2016 at North Cascades National Park, WA, USA. The vertical dotted-line marks the record-low snowpack in 2015.

Partnerships

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Publications

This report will be edited, reformatted, and submitted for publication in a peer-reviewed journal in March 2018. An oral presentation of this project will be broadcast online at noon (MST) on March 13, 2018 through the USGS Eco-lunch Seminar Series at the Northern Rocky Mountain Science Center in Bozeman, MT. An abstract of this project has been submitted for oral presentation of the project at the annual meeting of the Ecological Society of America in New Orleans in August 2018. A fact sheet for this project that is suitable for dissemination to the public as a hard copy has been provided with this report, and a webpage with this information will be available on the USGS website for the Northern Rocky Mountain Science Center.